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Response Properties of Chemoreceptors from the Medial Antennular Filament of the Lobster *Homarus americanus*

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Abstract. We determined the spectral tuning properties of 53 single cells from the medial antennular filament of the lobster *Homarus americanus*. Test stimuli were 15 single compounds and a mixture that included all 15 test compounds. Three main cell populations were found: hydroxyproline best (14 cells), taurine best (13 cells), and arginine best (11 cells). Most hydroxyproline and taurine best cells were narrowly tuned and had no consistent next best stimulus. In contrast, arginine best cells were generally broadly tuned and had consistent second (leucine) and third (lysine) best stimuli. Mixture suppression occurred in most cells. Responses of hydroxyproline, taurine, and arginine best cells to the mixture were 25%, 38%, and 50%, respectively, relative to the responses of these cells to their best compound alone (100%). In a second experiment, we tested 12 arginine sensitive cells with a series of arginine analogs. Most cells were broadly tuned and as a population showed a similar response ratio to arginine, leucine, and lysine.

Introduction

Amino acid receptors occur in the olfactory and taste systems of numerous species. Crustaceans have proved to be particularly useful models for investigating properties of such external amino acid receptors. Behavioral studies have identified stimulatory amino acids and described responses to these compounds in marine, freshwater, and semi-terrestrial species (Carter and Steele, 1982; Zimmer-Faust *et al.*, 1984; Johnson and Atema, 1986; Tierney and Atema, 1988; review: Ache, 1982). These studies have generally supported the idea that amino acid chemoreception is related to the detection of food. Electrophysiological studies, particularly with lobsters and crayfish, have provided additional information on the location, sensitivity, and specificity of single amino acid receptors. Two significant properties of lobster chemoreceptors have been identified. First, unlike most chemoreceptors that function in feeding behavior in vertebrates and insects, lobster cells are typically narrowly tuned. Many receptors respond strongly to only one or a few compounds (Derby and Atema, 1982b; Johnson and Atema, 1983; Johnson *et al.*, 1984). Second, most crustacean chemoreceptors display mixture interactions in which responses to a single compound are reduced or enhanced when this compound is presented in a mixture (Johnson and Atema, 1983; Johnson *et al.*, 1985; Gleeson and Ache, 1985). The discovery of these properties has generated new ideas about how chemoreceptor systems may resolve stimulus quality (Atema *et al.*, 1988; Derby and Atema, 1988).

Electrophysiological studies of crustacean chemoreception have primarily focused on cells in the lateral antennular filament (Shepheard, 1974; Johnson and Ache, 1978; Johnson and Atema, 1983; Derby and Ache, 1984a; Gleeson and Ache, 1985; Johnson *et al.*, 1985; Spencer, 1986) and in the walking legs (Bauer *et al.*, 1981; Derby and Atema, 1982a, b; Johnson *et al.*, 1984; Hatt, 1984). However, other structures, including the medial antennular filament, the antennae, and the mouthparts are also chemosensory (Ache, 1982; Derby and Atema, 1982c). Little is known about the specificity and sensitivity of chemoreceptors in these latter append-

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ages. Medial antennular filaments differ structurally from lateral filaments: they are shorter, more slender and, most significantly, they do not flick and lack aesthetasc hairs. The latter two features are thought to be important in orientation to chemical gradients (Reeder and Ache, 1980; Devine and Atema, 1982). Nonetheless, in the spiny lobster (*Panulirus argus*) medial filaments contain taurine receptors of equivalent specificity (Fuzessery *et al.*, 1978) and sensitivity (Fuzessery, 1978; Thompson and Ache, 1980) to those found in lateral filaments. Fuzessery (1978) reported that medial filament taurine cells fired more tonically than did lateral filament cells, and suggested that the two filaments may perform different behavioral functions. Thompson and Ache (1980), however, found no difference in firing pattern between medial and lateral filament cells. A resolution of these conflicting observations in *P. argus* has yet to be provided. For other crustacean species, lack of data precludes a comparison of receptor properties of lateral and medial antennular cells.

A complete understanding of how any species uses chemoreception to adapt behaviorally to its environment will require knowledge of the response spectrum and receptor properties (response pattern, tuning breadth, mixture interactions, adaptation and disadaptation rates) of all chemosensory appendages. This study contributes to our understanding of chemoreception in an important model species, the American lobster (*Homarus americanus*), by describing the responses of single chemoreceptor cells from the medial antennular filament to amino acids and related compounds.

Materials and Methods

Medial antennular filaments were excised and mounted in a two-compartment recording chamber. The distal portion of the filament, bearing chemoreceptive sensilla, lay in a cylindrical compartment (inside diameter 3 mm), and was continuously flushed by artificial seawater (ASW) at a rate of 20 ml/min. The lumen of the filament was perfused with oxygenated *Homarus* ringer (Govind and Lang, 1981) through a cannula inserted into the cut distal tip of the filament. Stimuli were injected into the ASW flow above, and perpendicular to, the antennular filament. To estimate the temporal dilution profile of a 50 μl dose of stimulus, we measured the change in conductance of flowing, deionized water (20 ml/min) after injecting 50 μl of a 1 M salt solution. Following injection, the stimulus contacted the antennule in approximately .3 s, and peaked within .5 s. At peak the stimulus was diluted 15 times relative to the injected concentration, and was washed out within 1.5 s.

The cut proximal end was immersed in a ringer bath, which was separated from the distal portion of the filament by a sylgard plug. The proximal six annuli were removed to expose the antennular nerve. We used a suction electrode to record extracellular activity from small nerve bundles. Chemoreceptor responses were amplified and displayed by conventional electrophysiological equipment, and stored on magnetic tape.

In the first experiment, we identified chemoreceptive cells by searching for axons that altered their spike activity in response to 50 μl doses of a mixture of 15 compounds (Fig. 1), all at an injected concentration of 10^{-4} M (total mixture molarity 1.5×10^{-3}). With the exception of two amino acids (histidine and asparagine), the test stimuli are those used in previous studies of *Homarus* chemoreceptors (Johnson and Atema, 1983; Johnson *et al.*, 1984) and were chosen to allow a direct comparison to the results of these studies. The 15 compounds were then tested singly in doses of 50 μl at 10^{-4} M to determine the response spectra for individual cells. Injected concentrations were diluted to approximately 7×10^{-6} M in the test chamber. Concentrations reported hereafter account for this dilution. Test compounds, including injections of 50 μl ASW, were presented in varied order with an interval of 60 s between each stimulus application. The mixture was presented at the beginning and end of each test series. We rejected a data series if the final mixture or best single compound presentation elicited a response less than 40% of the initial response (Johnson and Atema, 1983). Chemicals were dissolved in ASW and frozen in 20 ml vials until the day of use. All solutions were presented at room temperature (23 ± 3°C) and at a pH of 7.4 (±.2).

Dose-response relations were determined for cells responding best to hydroxyproline (Hyp), taurine (Tau), and arginine (Arg). Chemicals were tested in an ascending concentration series from 7×10^{-10} to 7×10^{-4}. Because some cells showed marked adaptation to high concentrations of chemicals, we allowed a longer interval of 2 min between stimulus presentations for all dose-response studies.

In the second experiment, we identified arginine-sensitive cells with a search stimulus of 7×10^{-6} M arginine. Using the protocol described above, we then tested these cells with each of the arginine analogs listed in Table I.

Response intensity was measured by counting the number of spikes which occurred following stimulus injection. Most responses (75%) were over within 5 s, and the remainder were over within 10 s. A response was considered over when two or more seconds passed without spike activity; occasional spikes outlying this interval were disregarded. Twelve cells were spontaneously active. For these cells, spike counts were corrected for each stimulus presentation by subtracting the number of spikes occurring in a prestimulus interval from the number occurring in a poststimulus interval of equal dura-

Table I

Compounds tested in Experiment 2

Compounds	Structural Formulas
L-Arginine	$COOH(NH_2)CH(CH_2)_3NHC(NH)NH_2$
L-Arginine HCl	$HCl\,COOH(NH_2)CH(CH_2)_3NHC(NH)NH_2$
L-Homoarginine	$COOH(NH_2)CH(CH_2)_4NHC(NH)NH_2$
ω-Nitro-L-arginine	$COOH(NH_2)CH(CH_2)_3NHC(NH)NHNO_2$
L-Arginine methyl ester	$COOCH_3(NH_2)CH(CH_2)_3NHC(NH)NH_2$
Argininic acid	$COOH(OH)CH(CH_2)_3NHC(NH)NH_2$
L-Citrulline	$COOH(NH_2)CH(CH_2)_3NHCONH_2$
L-Ornithine	$COOH(NH_2)CH(CH_2)_3NH_2$
L-Lysine	$COOH(NH_2)CH(CH_2)_4NH_2$
L-Leucine	$COOH(NH_2)CHCH_2CH(CH_3)_2$
L-Isoleucine	$COOH(NH_2)CHCHCH_3(CH_2)CH_3$
L-Norleucine	$COOH(NH_2)CH(CH_2)_3CH_3$
L-Valine	$COOH(NH_2)CHCH(CH_3)_2$
L-Norvaline	$COOH(NH_2)CH(CH_2)_2CH_3$

tion. We identified spikes from single chemoreceptors by analysis of recordings containing only one active cell or, in multiunit recordings, by discriminating cells on the basis of amplitude and waveform. Three cells that did not respond to the mixture (cells 8, 45, and 47; Fig. 2) were identified during the analysis of multiunit recordings.

Results

Experiment 1: general survey

Our analysis of the first experiment used 53 cells, all tested on the complete series of compounds and all clearly resolvable as single units. Best stimuli for the medial receptors were Hyp, Tau, and Arg. Hyp elicited responses from more cells than did any other single compound (Fig. 1A). However, Arg and Tau elicited a greater number of spikes across all cells than did Hyp (Fig. 1B). Three main cell populations were present: Hyp best (14 cells), Tau best (13 cells), and Arg best (11 cells). Also present were cells most responsive to ammonium chloride (NH_4; 4 cells), betaine (Bet; 4 cells), leucine (Leu; 1 cell), lysine (Lys; 1 cell), glutamine (Gln; 1 cell), proline (Pro; 1 cell), glycine (Gly; 1 cell), glutamate (Glu; 1 cell), and the mixture (1 cell).

Tuning properties to single compounds were highly variable, with some cells responsive to only one stimulus and others responsive to several or all stimuli (Fig. 2). Among the Hyp best cells, four (cells 1, 2, 3, and 4) responded only to Hyp. Most of the other cells gave weak responses to one or a few compounds in addition to Hyp, and one relatively broadly tuned cell responded to a total of eleven compounds. Among Tau best cells, four responded only to Tau (cells 15, 16, 17, and 18); five other cells (cells 19, 20, 21, 22, and 23) responded to five or fewer compounds. The remaining four cells (cells 24, 25, 26, and 27) were broadly tuned, responding to eight or more compounds. For Hyp best cells, some compounds were more often stimulatory than were others. For example, asparagine (Asn) elicited spikes from eight Hyp best cells, whereas alanine (Ala) was always nonstimulatory to these cells. However, no compound was consistently the second or third best stimulus for Hyp best cells. Likewise, for Tau best cells there were no consistent next best stimuli.

Arg best cells differed from Hyp best and Tau best cells in at least two major ways. First, Arg best cells generally responded with more spikes (mean number of spikes/response, 136; range, 7–246) than did Hyp best cells (mean number of spikes/response, 27; range, 8–55) or Tau best cells (mean number of spikes/response, 75; range 19–144). Second, Arg best cells were generally broadly tuned and had a consistent second best (Leu) and third best (Lys) stimulus. Some Arg best cells also responded to other compounds, particularly Gln, Bet, Pro, and Ala (Fig. 2); however, the order of effectiveness of these less stimulatory compounds was inconsistent. Although Arg, Leu, and Lys were always the first, second, and third best stimuli, respectively, there was much quantitative variability among cells in how stimulatory Leu and Lys were compared to Arg and to each other. Relative to the response to Arg (100%), the response to Leu ranged from 18% to 94%; the response to Lys ranged from 7% to 57%. The response to Lys, relative to Leu (100%), ranged from 14% to 80%. Because adaptation was common, some of this variability is probably ascribable to the order in which stimuli were presented.

Mixture suppression occurred in most cells (Fig. 3). Responses of Hyp, Tau, and Arg best cells to the mixture were 25%, 38%, and 50%, respectively, relative to responses of these cells to their best compound alone (considered 100%). Responses of NH_4 (32%) and Bet (25%) best cells to the mixture were likewise less than responses to the best compounds alone. Differences were significant for all cell types (Wilcoxon matched-pairs signed-ranks test, $P < .01$).

Dose-response functions for six Hyp and five Tau best cells are shown in Figure 4. One cell responded to Hyp at 7×10^{-10} *M* (response = 6 spikes), but thresholds of other cells were at least an order of magnitude higher. For Tau best cells, one cell responded to Tau at 7×10^{-10} *M* (response = 4 spikes), and most others responded at 7×10^{-9} *M*. All Hyp and Tau best cells had a response range which covered at least three log units.

Experiment 2: arginine cells

We tested the complete series of compounds listed in Table I on 12 cells. Eight cells appeared to be of the same

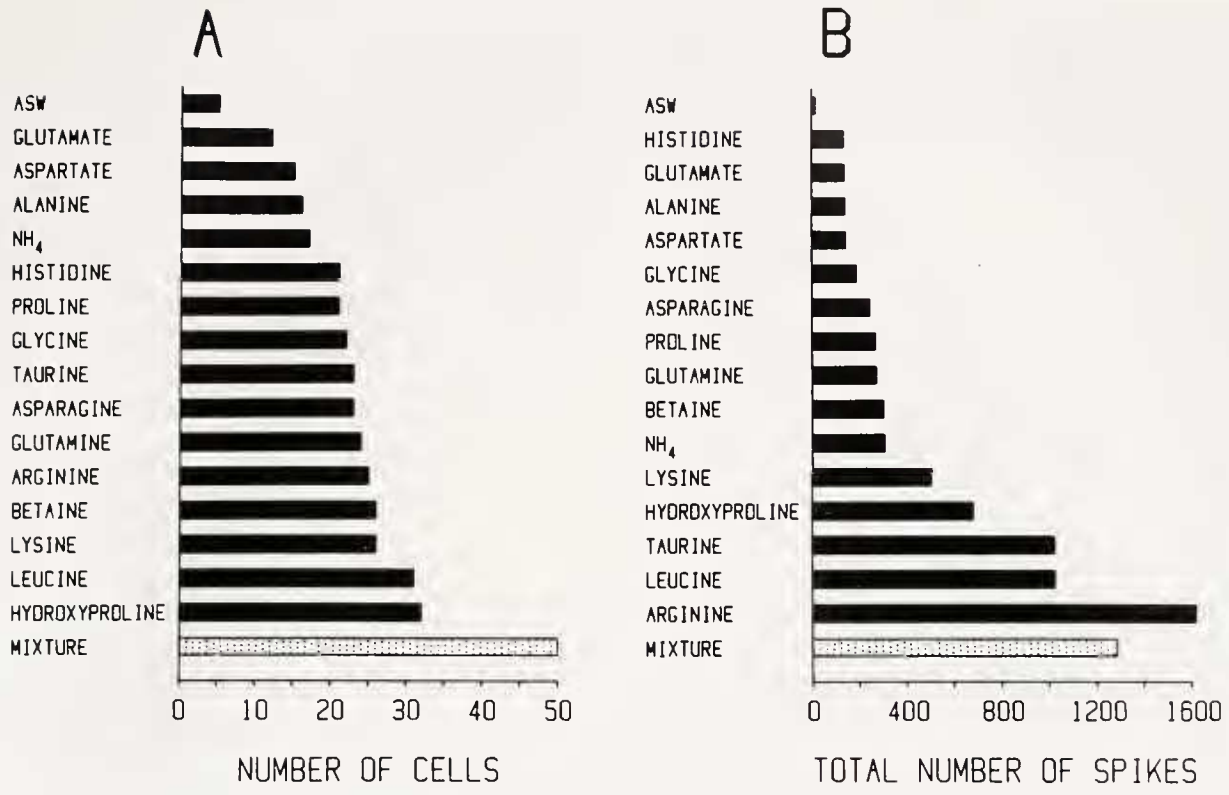

Figure 1. Stimulatory effectiveness of single test compounds, the mixture and ASW on medial antennular filament chemoreceptors from *H. americanus*. All amino acids tested were L isomers. A. Number of cells that responded with one or more spikes to each compound. B. Total number of spikes elicited by each compound (all spikes of all cells).

type identified previously (cells 1–8). These cells generally responded strongly to their best stimulus (mean number of spikes/response, 138; range, 15–283) and were broadly tuned, responding to all or most of the stimuli (Figs. 5, 6). Although these cells were not identical in their responses, a general order of stimulus effectiveness was discernable. Arg and Arg-HCl were always the most stimulatory compounds. Arginine methyl ester, Leu, and isoleucine were typically the third, fourth, and fifth best stimuli, respectively. Other consistently stimulatory compounds were valine, homoarginine, norleucine, norvaline, and Lys. The remaining compounds—citrulline, nitroarginine, ornithine, and argininic acid—elicited weak responses from some cells.

The four additional cells identified by the arginine search stimulus differed qualitatively from the cells described above (Fig. 6). The best stimuli for these cells were argininic acid (cells 9 and 10), Lys (cell 12), and Leu and homoarginine (cell 11). The order of effectiveness of other stimulatory compounds was different in each cell. The response elicited by the best stimulus was much lower in these cells (mean number of spikes/response, 25; range, 5–52) than in the Arg best cells described above.

Discussion

Our results provide the first description of the response spectra of single medial antennular chemoreceptor cells from *Homarus americanus*. These results contribute to a growing literature on how single chemoreceptors respond to amino acids in organisms from bacteria to mammals. More specifically, test stimuli used in the present study included many compounds previously tested on *H. americanus* and *P. argus* lateral antennules and legs (Shepheard, 1974; Fuzessery *et al.*, 1978; Johnson and Ache, 1978; Derby and Atema, 1982a, b; Johnson and Atema, 1983; Johnson *et al.*, 1984), and allow a comparison of response properties of different chemosensory organs. The following properties are briefly discussed below: response spectra of different organs, response magnitude, response duration, tuning breadth, and mixture suppression.

A major similarity in the response spectra of medial and lateral antennular filaments were the prominent populations of Hyp and Tau best cells found in both organs (Shepheard, 1974; Fuzessery *et al.*, 1978; Johnson and Atema, 1983). Like the lateral filaments of *H. americanus* (Johnson and Atema, 1983), the medial filaments

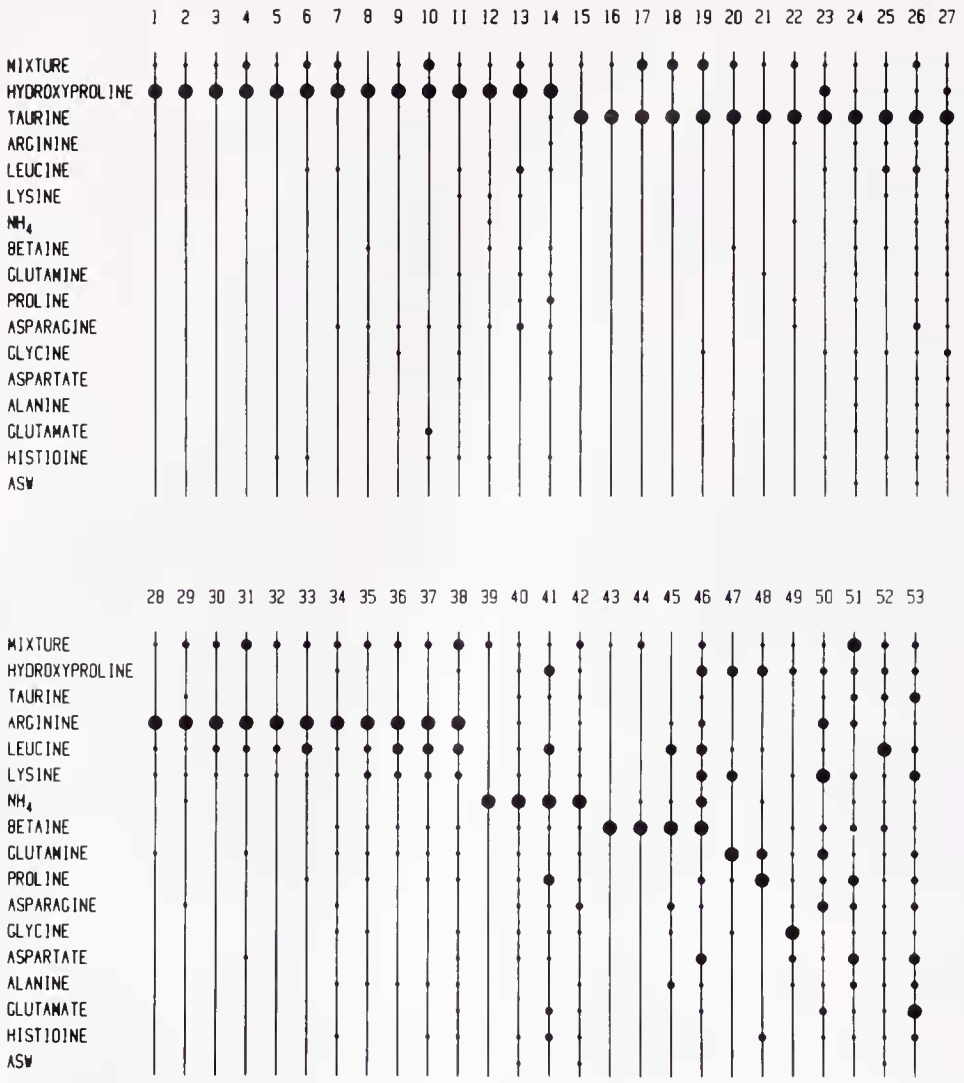

Figure 2. Tuning properties of 53 chemoreceptors from medial antennular filaments. Each cell's responses are normalized to the maximum response. A continuous line indicates no response, the smallest dots indicate less than 30% of the maximum response, second largest dots indicate between 30% and less than 70%, third largest dots indicate between 70% and less than 100%, and the largest dots indicate 100%.

also possessed a few cells most responsive to other compounds (*e.g.*, NH_4, Bet, Pro). Contrary to previous results (Shepheard, 1974), we found that medial filament receptors were not highly responsive to Glu. Medial and lateral filaments also differed in that the former, but not the latter, possessed a significant population of Arg best cells. For leg receptors, best stimuli were Glu, NH_4, Bet and Hyp (Derby and Atema, 1982a, b; Johnson *et al.*, 1984). Smaller populations of cells most responsive to other compounds (*e.g.*, Lys, Tau, Leu: Johnson *et al.*, 1984; Gln, Arg: Derby and Atema, 1982b) were also present. This brief survey demonstrates that, while responses of lobster antennules and legs were not identical, considerable overlap in qualitative sensitivity does appear to exist in the lobster's chemoreceptor organs.

Hyp and Tau best cells from different appendages were similar in the relative magnitude of their responses to their best compound. Hyp best cells in both branches of the antennules typically responded to Hyp with relatively few spikes (mean number of spikes/response to a 1-second pulse of 3×10^{-6} *M* Hyp = 27 for medial antennular receptors and 30 for lateral antennular receptors, Johnson *et al.*, 1985). Responses of Tau best cells were generally stronger (mean number of spikes/response to a 1-second pulse of 3×10^{-6} *M* Tau = 75 for medial antennular receptors and 89 for lateral antennular receptors). The low responses of Hyp best cells suggest that the best stimulus for these receptors may be a compound as yet unidentified. Alternatively, Hyp cells may represent a distinct population of cells that occur in all sensory or-

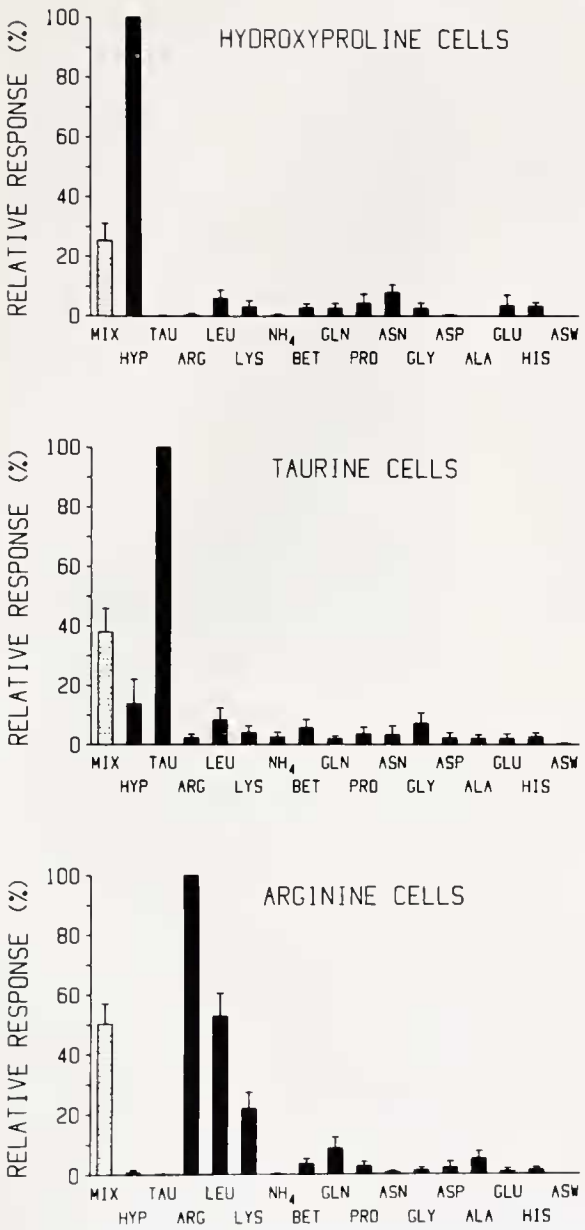

Figure 3. Responses of the three main chemoreceptor cell populations found in the medial antennular filaments of *Homarus americanus*. Bars indicate mean response + SEM of all cells in each population, normalized to the response to the best stimulus (=100%).

gans and which, for reasons perhaps unrelated to stimulus-receptor binding affinities, have a relatively low firing rate (Johnson *et al.*, 1984, 1988).

We found no difference in discharge pattern between medial and lateral filament receptors. Medial antennular receptors typically responded to increasing stimulus concentration with a gradual increase in spike number and response duration (Fig. 4). A similar discharge pattern was observed in *H. americanus* lateral receptors (Johnson *et al.*, 1985). Likewise, Thompson and Ache (1980) found no difference in response duration between medial and lateral filament receptors in *P. argus*. These results contrast with those of Fuzessery (1978) who reported that, for taurine sensitive cells in *P. argus*, responses of medial receptors were tonic, whereas responses of lateral receptors were phasic.

Despite similarities in response spectrum, and in the response magnitude, pattern, and sensitivity of individual cells, the medial and lateral antennular filaments are not behaviorally equivalent. Ablation experiments demonstrated that both *P. argus* (Reeder and Ache, 1980) and *H. americanus* (Devine and Atema, 1982) rely on the lateral filaments for orientation to concentration gradients of food related chemicals. These experiments found that the medial filaments were unnecessary and insufficient for this purpose. At present the function of the medial filaments is unclear, though the results of the present study suggest that the apparent lack of behavioral reliance on medial filaments is not due to a lack of competent receptors. If these structures are in fact behaviorally important as chemoreceptive organs, their importance may be due to the presence of unique receptors not used for orientation within laboratory tanks, and as yet unidentified in physiological tests. Also, the experiments cited above tested animals within two days following lateral antennule ablation. Conceivably, given a longer recovery time, medial filaments may develop a capacity to mediate behaviors such as orientation and thereby functionally replace, at least in part, lost lateral receptors. Such enhancement of chemoreceptor function occurred in crabs in which the sensitivity and behavioral impor-

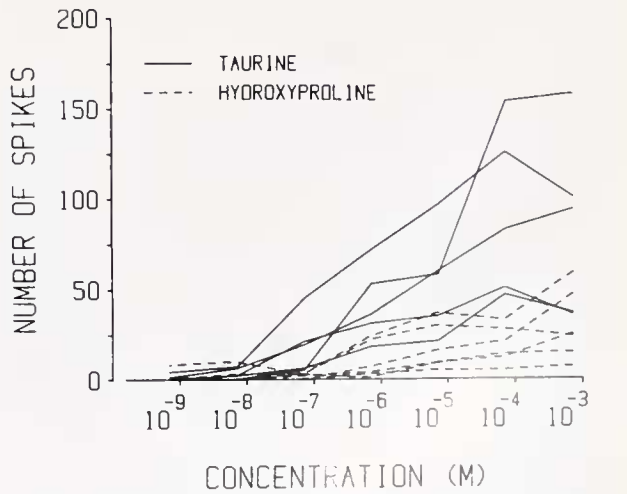

Figure 4. Dose-response functions for six Hyp and five Tau best cells from medial antennular filaments of *Homarus americanus*. Stimuli were tested in an ascending concentration series, with 2 min intervals between stimulus presentations

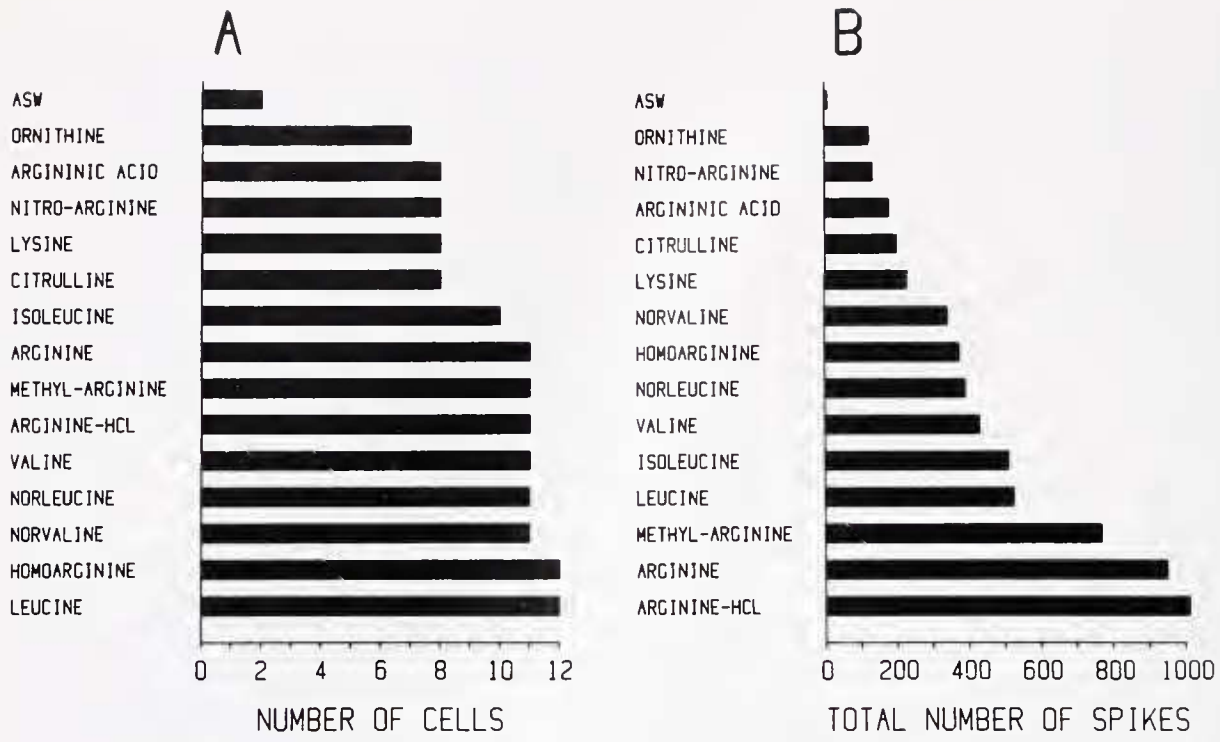

Figure 5. Stimulatory effectiveness of single test compounds and ASW on arginine-sensitive cells in medial antennular filaments from *Homarus americanus*. A. Number of cells which responded with one or more spikes to each compound. B. Total number of spikes elicited by each compound (all spikes of all cells).

tance of dactyl chemoreceptors became increased 7 to 10 days after antennule ablation (Hazlett, 1971).

Narrowly tuned cells are a predominant feature of *H. americanus* lateral antennules (Johnson and Atema 1983) and legs (Derby and Atema 1982b; Johnson *et al.*, 1984). Similarly, many medial filament cells responded strongly to only one compound. Ten cells (four Hyp, four Tau, one Bet, and one NH_4) responded exclusively to one compound (Fig. 2). An additional 14 cells responded only weakly to other compounds (response to a second best compound was less than 30% of the cell's maximal response; Fig. 2). A comparison of H-metric values calculated from the present data and from lateral antennular filaments (data from Johnson and Atema, 1983), indicates that Hyp and Tau best cells are tuned similarly in the two filaments (Table II). The mean H-metric value for Hyp best cells in leg receptors, however, is higher than the values for antennular receptors, suggesting that as a population the former are more broadly tuned than the latter.

Arg best cells had a relatively broad response spectrum and, in contrast to other *H. americanus* chemoreceptor cells, displayed a consistent order of responsiveness to stimulatory compounds. In our initial survey, Leu and Lys were always the second and third best stimuli, respectively. In our second experiment, Leu was less effective than arginine methyl ester, and Lys was less effective than arginine methyl ester, Leu, isoleucine, valine, norleucine, homoarginine, and norvaline. However, despite differences in test compounds, the ratio of responses of Arg, Leu, and Lys were similar in the two experiments. In experiment 1, overall responses to Leu and Lys were 49% and 21%, respectively, relative to the response to Arg (100%); in experiment 2, responses to Leu and Lys were 54% and 22%, respectively, relative to the response to Arg (100%).

Arg best cells from legs were also sensitive to Lys, with Lys being 100 to 1000 times less stimulatory than Arg (Derby and Atema, 1982b). Our dose response data for Arg, Leu, and Lys indicated that medial filament Arg best cells were likewise approximately 100 to 1000 times less sensitive to Lys than to Arg ($n = 4$; data not shown). Further comparison of Arg cell types must await data on responses of leg receptors to Leu and other compounds stimulatory to medial filament cells. Tau best cells from *P. argus* antennules also had a consistent order of responsiveness to certain Tau analogs (Fuzessery *et al.*, 1978). However, unlike Arg best cells which responded to an array of structurally diverse compounds, Tau cells from *P. argus* responded only to a few compounds closely related to Tau.

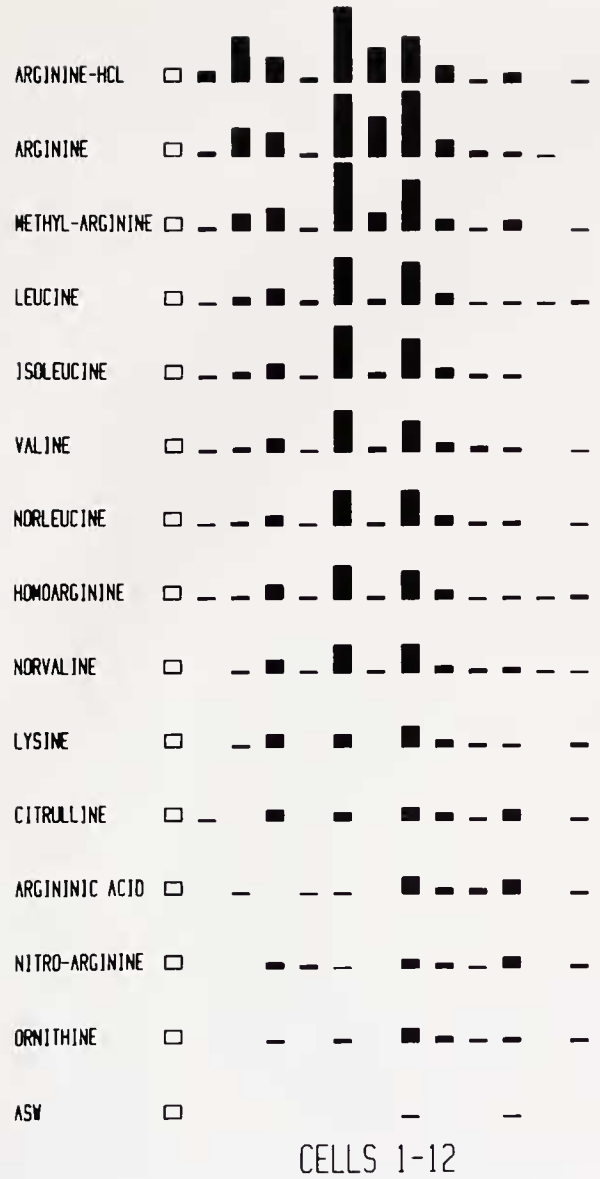

Figure 6. Responses of 12 arginine sensitive chemoreceptors from medial antennule filaments of *Homarus americanus* to 14 single compounds and ASW. Bars indicate the number of spikes each cell gave in response to each compound. Open calibration bars at far left indicate response of 50 spikes.

The functional significance of the distinctively tuned Arg best cells is unknown. Amino acid receptors of aquatic animals are commonly assumed to function as detectors of food related compounds. Narrow tuning may enhance the ability of receptors to perceive important stimuli by reducing interference from other possibly cross-adapting compounds (Fuzessery *et al.*, 1978; Johnson *et al.*, 1984). It is not clear, however, why this explanation applies only to certain amino acids, and only to certain species. In crayfish leg receptors, for example, all amino acid sensitive cells were broadly tuned, with the order of stimulus efficacy consistent from cell to cell (Bauer *et al.*, 1981; Hatt, 1984). Chemoreception studies necessarily test only a minute fraction of potentially stimulatory compounds. Conceivably the striking difference in tuning breadth between Arg best cells and other *H. americanus* cells is an artifact resulting from the selection of test compounds. Thus, perhaps Glu best cells possess second, third, *etc.* best stimuli, but the appropriate compounds were not included in tests which defined the response spectrum of these cells.

Mixture interactions, both synergistic and suppressive, occur in the chemoreceptor systems of invertebrates and vertebrates (Shiraishi and Kuwabara, 1970; Bartoshuk, 1977; Dethier, 1977; Hyman and Frank, 1980a, b; Cagan, 1981; Gillan, 1982, 1983). In the lobster olfactory pathway mixture suppression occurs in peripheral receptors (Johnson and Atema, 1983; Gleeson and Ache, 1985; Johnson *et al.*, 1985) and central interneurons (Derby and Ache, 1984a, b). Examples of peripheral suppression are Hyp and Tau best cells from lateral antennular filaments which responded better to their best compound alone than to this compound within a mixture (responses were 58% for Hyp and 69% for Tau within the mixture, relative to 100% for responses to the best compound alone; Johnson and Atema, 1985). Mixture suppression in medial filament cells was even more pronounced for Hyp and Tau best cells (responses to these compounds within the mixture were 25% and 38%, respectively; response to compounds alone = 100%). Arg best cells, however, showed less pronounced suppression (50% = Arg alone; 100% = mixture). Possibly the latter phenomenon is attributable to the presence within the mixture of at least two additional compounds (Leu and Lys) which reliably, and often substantially, stimulated Arg best cells. Thus, during mixture presentations Leu

Table II

Response breadth of hydroxyproline and taurine best cell populations in the medial antennular filament, lateral antennular filament and the legs of Homarus americanus *measured by the H-metric**

Cell populations	Mean	Median	Range	N
Hyp (medial)	.1906	.1674	0–5744	14
Hyp (lateral)	.2190	0	0–.8717	17
Hyp (leg)	.4376	.4307	0–.6841	9
Tau (medial)	.2682	.1021	0–.8746	13
Tau (lateral)	.2399	.1328	0–.8822	7

N is the number of cells.

* $H = -K \sum_{i=1}^{n} P_i \log_{10} P_i$; where H = entropy measure of response breadth, K = scaling constant (−0.8977, for 13 compounds; sucrose, ethanol, Asn and His were eliminated from the analysis because they were not used in all three studies), P_i = the proportional response of each of the 13 test compounds (Smith and Travers, 1979).

and Lys could occupy receptor sites and cause moderate cell stimulation while excluding a proportion of the suppressive compounds contained in the mixture.

Acknowledgments

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